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Effect of temperature on development, reproduction, longevity and grain weight losses of the Khapra beetle, *Trogoderma granarium*

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ABSTRACT:

The khapra beetle, *Trogoderma granarium* (Coleoptera: Dermestidae) is a cosmopolitan species and one of the most destructive insect pests of stored grain products, and dozens of other commodities, with great importance. Temperature is a major driver of key insect functions, involving development, survival, longevity, and reproduction. Therefore, this work designed to study effect of different temperature regimes (22°, 27°, 32°, 37º, and 42ºC) on development, reproduction, longevity and grain weight loss of *T. granarium* using the whole wheat grains as a feeding substrate. The developmental time and rate were used to estimate the lower developmental threshold (T_0) and then the degree-days (dd's) required to compete development. Temperature had significant effects on total development, longevity, life span, fecundity, and weight loss of *T. granarium*. Except at 42°C, the survival rates of immature stages increased as the temperature increased. As well, sex ratio biased for females as temperature increased from 22º to 37ºC, but at 42ºC the sex ratio biased for males. The lowest T_0 was recorded for male's life span, followed by that for female's life span. On average, the total life cycle, and female and male life spans of *T. granarium* beetles needed 602.0 ± 15.08, 938.14 ± 31.86, and 950.23 ± 22.34 dd's, respectively to complete their development. This study recommends the wholesalers to use temperature of 42ºC or above to protect stored wheat, since it increased mortality rates, reduced fecundity and longevity, and minimized wheat weight loss by *T. granarium*.

INTRODUCTION

The khapra beetle, *Trogoderma granarium* Everts (Coleoptera: Dermestidae) is a cosmopolitan species that is cause severe damage to stored grain products and dozens of other commodities, with great importance (**Finkelman *et al*., 2006; Hosseininaveh *et al*., 2007; Stibick, 2007; Burges *et al*., 2008; Hagstrum and Subramanyam, 2009**). In fact, *T. granarium* has been designated as a grade A2 quarantine pest and is recognized among the world's 100 most important invasive species (**Lowe *et al*., 2000; Myers and Hagstrum, 2012; Yadav and Srivastava, 2017**). Economically, its importance is not only due to the serious damage it can cause to stored dry goods, but also to the export constraints that countries face when they have colonized populations of this pest.

The khapra beetle is called a 'dirty feeder' and is an external (primary)-infesting pest in which an individual partially destroys grain kernels more than it actually requires to complete growth (**Stibick, 2009; Myers and Hagstrum, 2012**), enhancing its successful competition against native competitors that may share the same space. The larval stage is the most dangerous, as it greatly reduces the quality of stored grains, whereas the adults usually do not feed or feed very little (**Ahmad *et al*., 2022; Shahbazi *et al*.,**

2022). The larvae consume the seed embryo before the kernel, leaving behind only the pericarp; and it can greatly reduce the value of stored commodities. Although *T. granarium* is a primary pest, its young larvae feed on cracked grains, whereas its older larvae feed on whole grains (**EPPO, 1997; Athanassiou *et al*., 2016**). It can cause a loss in grain weight ranging between 5-33% and can reach to 73% in severe infestations (**GISD, 2015**).

Temperature, relative humidity, light, crowding, competition with other species, and food quantity and quality are the primary physical factors that affect *T. granarium* growth (**GISD, 2015**). The variations in such parameters can predict the occurrence time of insect generation with high accuracy (**Bale *et al*., 2002**). However, temperature is the major engine of key functions of insects, including growth, survival, movement, and reproduction. Among these, development is of particular importance in applied entomology because its importance for building phenological models (**Golizadeh and Zalucki, 2012**). This insect pest may reproduce from one to more than ten generations annually depending on the temperature (**Ramzan and Ghahal, 1986; GISD, 2015**). Many models have been developed to address the challenge of describing insect responses to temperature over the past century. Recent developments have addressed the significance of thermal performance curves in ecology and entomology, their inherent assumptions are recognized (**Sinclair *et al*., 2016**). The most popular thermal performance curve is based on the thermal constant theory that developed for plant sciences (i.e., completing the growth of a certain stage requires an accumulation of energy measured in day-degrees above the lower development threshold) (**Rebaudo and Rabhi, 2018**).

Two key parameters that describe the relation between temperature and insect development are the lower developmental threshold, T_0 (the temperature below which no development happens) and the thermal constant, K [(the cumulative number of degree-days (DDs)] required to complete a given developmental stage above T_0 (**Higley *et al.*, 1986**). The relationship between temperature and developmental rate (inverse of developmental time) is a linear function until the upper limit of the appropriate temperature is reached (**Wagner *et al*., 1984**). Each individual of an insect species must accumulate a certain amount of heat before it can move the next developmental stage. Once the thermal constant is known, the key biological aspects of pest life history, such as adult emergence, could be predicted by estimating the accumulation of heat, i.e DDs. The number of generations of a pest annually will also depends on the total accumulating annual units of heat accumulation (**Yamamura and Kiritani, 1998**). Degree-day models were used under different temperatures for estimating the thermal developmental constant of different stored product insects and moths under (**Subramanyam *et al*., 1991**).

Many studies have documented how this pest performs well in warmer temperatures (**Kavallieratos *et al*., 2017a; Lampiri *et al*., 2021**). Under hot and dry conditions, this pest becomes more prevalent, where very heavy infestations can develop (**IPPC, 2016**). The total development may be as short as 26 days (temperature 32–35°C) or as long as 220 days in a suboptimal temperature. However, the optimum temperature at which development of *T. granarium* occurs is 35°C (**Riaz *et al*., 2014; Yadav and Srivastava, 2017**). Identifying the unfavourable temperature that hinders the development and reproduction of the khapra beetle will enable the scientists and wholesalers to implement appropriate measures to protect stored wheat and other commodities by minimizing storage losses.

MATERIAL AND METHODS

1. INSECT CULTURE

The initial population of the Khapra grain beetle, *T. granarium* was obtained from the Stored Product and Grain Pests Department at Sakha Research Station, Plant Protection Research Institute, Agriculture Research Center, Giza. The present experiments were carried out in the laboratory belonging to the Economic Entomology Department, Faculty of Agriculture, Mansoura University. The wheat kernels were used for maintaining the insect rearing. Before using, these kernels were sterilized at -20ºC for three days to eradicate any mites or hidden insect stages (**El-Sabaay, 1988**). The used kernels were then transferred to an incubator adjusted to 37 ± 1 ºC and 60 ± 5% RH for two weeks to obtain an equilibrium moisture content (**Ezz, 1976**). These grains were used to rearing the insect by introducing groups of about 300 males and females of the insect adults (150 pairs of the beetle) to 200 g of wheat kernels in plastic jars (20 × 10 cm) which covered by muslin and allowed for the pairs to mate and oviposition for ten days, then the adults were excluded. The mass culture for this insect species were monitored for two generations before using in the current experiments.

2. EFFECT OF TEMPERATURE ON DEVELOPMENT, REPRODUCTION, LONGEVITY AND GRAIN WEIGHT LOSSES OF *T. granarium*

Five incubators adjusted to 22°, 27°, 32°, 37°, and 42 ± 1 ºC were used. The relative humidity was adjusted in all incubators to be 60 ± 5% with full darkness. The whole wheat grains of the variety Gemiza 12 was used as a feeding substrate. Ten pairs of the beetle were isolated from the culture, confined in a 9.0 cm Petri dish containing 5 gm of the grains, and kept at each temperature regime for 24 hr. For study the development, ten newly deposited eggs, were collected from beetles kept at a certain temperature, placed in each Petri-dish (9 cm in diam.). Each dish contained 5 gm of the wheat grains. Ten replicates were used for each temperature regime. The development was monitored daily. The duration of all immature stages, the number of successfully emerged adults, immature survival, and sex ratio were recorded and estimated at each temperature regime. The difference in weight between initial and final weights (i.e. weight loss) after adult emergence was estimated.

Once adult emerged, five pairs (males and females) were collected from each treatment. Each pair was introduced in a Petri-dish (5 cm in diam.) and allowed to mate and oviposit at the same rearing temperature. These pairs were monitored daily to exactly recorded the ovipositional periods (preoviposition, oviposition, and post-oviposition). The adult longevities and life span of male and female *T. granarium* were then estimated. The F1 progeny was recorded at each temperature.

The developmental time and rate were used to estimate the lower developmental threshold (T_0). The regression line between the developmental rates, y (determined as the inverse of the development duration, D, at a specific temperature, 1/D) and the temperature regimes, x, has been approved based on the assumption that the relationship between both variables is linear above T_0 (**Fletcher, 1989**). To set up this relationship, T_0 value was determined by dividing the x-constant by the slope of regression line, $T_0 = -a/b$ (Arnold, 1960). Accordingly, a certain number of the heat (thermal) units (often expressed as day-degrees) above this lower threshold is needed to complete development (**Fletcher, 1989**). The thermal constant K, the amount of heat units needed for development of 50% of population in a specific life stage was determined at each specific temperature (T) as $K = D (T – T_0)$ (Arnold, 1960).

3. STATISTICAL ANALYSIS

Data were first tested for passing normality (Shapiro–Wilks test) and equality of variance (Levene's test) tests before ANOVA took place. Effect of temperature on various developmental parameters (total developmental time, survival, longevity, fecundity, weight loss, thermal requirements) were tested using One-way ANOVA. Means were separated by Fisher's LSD test (α = 0.05). Analyses were conducted using the SigmaStat functions of SigmaPlot, v.12 (Systat, 2011).

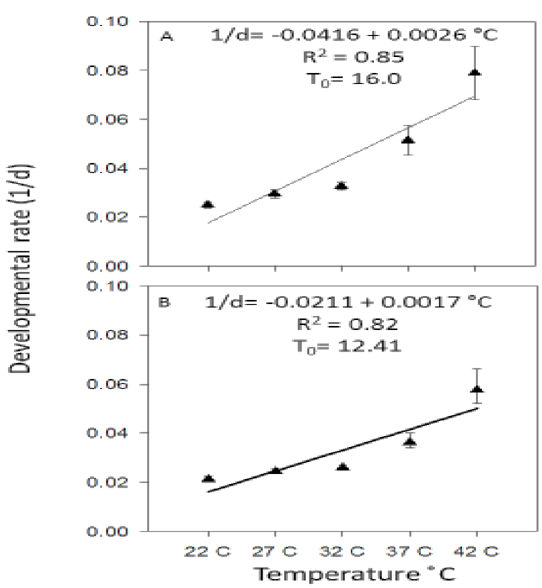
RESULTS

As temperature increased, the development of immature stages (egg-pupa), total development (egg-adult), female and male longevities, and female and male life spans decreased. Temperature had significant effects on development of immature stages ($F_{4,49} = 318.6$, $P < 0.001$), total development ($F_{4,49} = 222.02$, $P < 0.001$), preoviposition, oviposition, and postoviposition periods ($F_{4,49} = 12.48$, $P < 0.001$; $F_{4,49} = 10.61$, $P < 0.001$; and $F_{4,49} = 12.65$, $P < 0.001$, respectively), female and male longevity ($F_{4,49} = 21.19$, $P < 0.001$ and $F_{4,49} = 20.54$, $P < 0.001$, respectively), female and male life spans ($F_{4,49} = 211.9$, $P < 0.001$ and $F_{4,49} = 189.80$, $P < 0.001$, respectively), weight loss ($F_{4,49} = 31.74$, $P < 0.001$), and fecundity per capita ($F_{4,49} = 30.93$, $P < 0.001$). Except at the higher temperature (42 °C), as the temperature increased, the survival rates of immature stages increased. The maximum weight loss (g) was estimated at 37.0°C and the minimum was at 42°C. Accordingly, the maximum percentage of healthy grains (88.2%) was estimated at 37.0°C and the minimum (74.6%) was recorded at 42°C. As well, sex ratio biased for females as temperature increased from 22º to 37 ºC, but at 42 ºC the sex ratio biased for males (**Table 1**).

The rate of development for immature stages, total development, and female and male life spans of the Khapra beetle increased with increasing temperature

(**Figs 1 and 2**). The highest T_0 was estimated for immature stages, followed by the total development (egg-adult). The lowest T_0 was recorded for male's life span, followed by that for female's life span. The coefficient of determination (R^2) ranged from 0.82 to 0.86 (**Table 2**). There was an inverse relationship between lower developmental threshold (T_0) and thermal units (dd's). Therefore, the highest average values of degree days (dd's) were for male's life span, followed by female's life span (**Table 3**). Temperature had significant effects on thermal unites required for development of immature stages ($F_{4,49}$ = 72.09, P < 0.001), of total life cycle ($F_{4,49}$ = 53.11, P < 0.001), and life span of female and males ($F_{4,49}$ = 19.55, P < 0.001 and $F_{4,49}$ = 29.68, P < 0.001, respectively). Thermal requirements were higher for development of immature stages, life cycle, and life span of female and males at 32 °C than other temperature regimes. Whereas the lower values were at 42 °C (**Table 3**). On average, the total life cycle, and female and male life spans of *T. granarium* beetles needed 602 ± 15.08, 938.14 ± 31.86, and 950.23 ± 22.34 dd's, respectively to complete their development.

Fig. 1. Linear relationship between developmental rates (± SE) of immature stages [egg-pupa (A)] and total development [egg-adult (B)] for the Khapra beetle, *Trogoderma granarium*, and temperature.



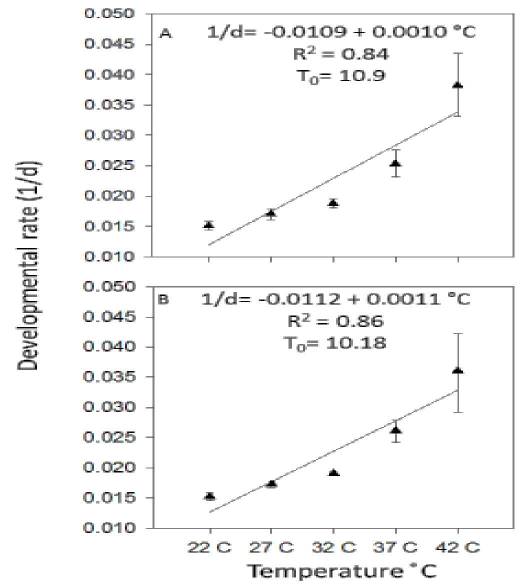


Fig. 2. Linear relationship between developmental rates of female (A) and male (B) life spans of Khapra beetle, *Trogoderma granarium*, and temperature.

DISCUSSION

Specifically, temperature-dependent development and survival of an insect species are fundamental parameters of life history, influencing its abundance across space and time (**Son and Lewis, 2005; Kontodimas *et al*., 2007; Papanikolaou *et al*., 2014**). These biological parameters are frequently examined in insect pests, because of their effect in the management strategies. The relationship between temperature and insect development is typically described by either a linear or a nonlinear curve, specified by the thermal thresholds (**Wagner *et al*., 1984; Fletcher, 1989; Azrag *et al*., 2017**). Further, thermal summation describes the amount of heat required to complete a developmental process and mostly it is estimated as DDs (**Higley *et al*., 1986; Honek, 1996**).

This pest prefers dry and hot habitats, and can grow at a temperature ranged from 20° to 41 °C (**Burges, 1962**). The development period (Egg-adult) declined significantly with increasing temperature (**Odeyem and Hassan, 1993**). It has a short period of about 13 days at 42 °C that raises with a decline in temperature below 42°C, until 22°C, where the development was the longest (**Yadav and Srivastava, 2017**).

It can reproduce efficiently at a minimum temperature of 24°C, but optimum range is 33-37 °C (Howe, 1965). In this study, 32-37ºC seems to be the preferred range for *T. granarium* development, however 37ºC seems to be the optimal because immature development has the highest rate of survival. Larval survival can be achieved highly when it fed on whole or crushed wheat flour (**Arain *et al*., 2006**). The survival rate is decreased considerably at 42 °C close to that reported at 40 °C (**Hadaway, 1956, Yadav and Srivastava, 2017**), but is not declined at 22 °C. In this study, 22ºC seems to be the lower limit for development and survival of *T. granarium*, as the survival declined considerably at 20°C (Riaz *et al*., 2014). Oviposition period tends to decrease with an increase in temperature °C (**Hadaway, 1956; Aldryhim and Adam, 1992**) with the longest period was at 22°C. For instance, oviposition period can be completed after 6.6 days at 40°C but, can be extended up to 22 days at 22°C. Female fecundity of *T. granarium* decreased significantly at low and high temperature, (**Burges, 2008**). Temperature of 37ºC seems to optimal. The highest lifetime fecundity was near to 51.0 eggs per female at 37ºC. Under optimal conditions, female fecundity is between 30 and 50 eggs (**Hadaway, 1956**). For example, fecundity was 43 eggs/female and developmental period of larval-pupal stage was 51.5 days at 25 ºC (**Hadaway, 1956**). The lowest fecundity was at 23.0ºC. At or below 20 °C, no eggs are laid (**Hadaway, 1956, Odeyem and Hassan, 1993**). The female and male longevity increases with a decrease in temperature (**Hadaway, 1956; Aldryhim and Adam, 1992; Burges, 2008; Riaz *et al*., 2014**).

In general, these results are similar to those of (**Burges, 2008**) who reported that, temperature above 40ºC is unfavourable for khapra and the favourable temperature lies between 30º and 40ºC. High temperature causes a number of adverse biochemical changes and have lethal effects in insect (**Neven, 2000**).

The maximum weigh loss of 25.4% caused by *T. granarium* larvae was estimated at 37.0ºC, and the minimum of 11.8% at 42.0ºC. Accordingly, the maximum healthy grain (88.2%) was recorded at 42ºC. (**Ahmad *et al*., 2014**) reported that the weight loss caused by *T. granarium* was 19.25, 16.0, 14.23 and 0.11% at 22º, 32º, 34º and 41 ºC, respectively. The results are also in agreement with (**Navarro *et al*., 1978 and Ahmedani *et al*., 2011**). These results show that, 42 ºC is not suitable for the production of khapra beetle. This results are consistent with those reported by (**Ahmad *et al*., 2014**).

Although the development of *T. granarium* has accelerated at 42°C, all other traits were the worst. Thus, maintaining stored wheat at 42°C or higher is a safe, environmental friendly physical method for controlling *T. granarium* in a temperate climate, since most stored product insects will not able to survive more than 24 h at 40°C, 12 h at 45°C, 5 min at 50°C, and 1 min at 55°C (**Fields, 1992**).

The lower temperature limits influence not only development of a species population, but also the activity of species (respiration, movement, sound production, etc.) and its survival (**Fields,1992**). Unfortunately, there are no enough data about the lower developmental threshold and thermal requirements for *T. granarium* to be used in explaining our findings. The average lower development threshold (LDT) for stored product pests varied among orders: the lowest was reported for Acari (6.8 ◦C) and Diptera (8.1ºC), followed by Lepidoptera (11.3ºC) and Psocoptera (13.8ºC), and the highest was reported for Coleoptera (14ºC) and Blattodea (15ºC) (see Stejskal *et al*., 2019). In this study, the lower developmental threshold for the total developmental period (egg-adult) of *T. granarium* is 12.41ºC. The lower developmental threshold (T_0) ranged between 15.5-18.5ºC for *Trogoderma anthrenoides* (**Kiritani, 1997; Jarosik *et al*., 2011**), 10.2-10.8ºC for *T. glabrum* (**Kiritani, 1997**), 13.3-13.9ºC for *T. granarium* (**Imura, 1990; Kiritani, 1997; Beckett, 2011**), 11.4-15.4ºC (Kiritani, 1997; Jarosik *et al*., 2011) for *T. inclusum*, 12.2-15.5ºC for *T. variabile* (**Kiritani, 1997; Jarosik *et al*., 2011**), 17.0-17.1ºC for *T. versicolor* (**Imura, 1990; Kiritani, 1997; Beckett, 2011; Jarosik *et al*., 2011**). The difference in T_0 is natural and is due to differences in temperature ranges that used in these studies and in geographical strains and species of *Trogoderma*.

The growth and development of an insect species are highly associated with its thermal thresholds and thermal summation (**Papanikolaou *et al*., 2013**). In this study, 602.77 degree-days above a threshold of 12.4ºC are required to complete preimginal development from egg until adult emergence. (Skourti *et al*., 2019) estimated 659.7 degree-days above a threshold of 16.9ºC for *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae) to complete immature development (egg- adult).

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The authors declare that they have no conflict of interest

AUTHORS CONTRIBUTION:

All authors developed the concept of the manuscript. Almayar wrote the manuscript and achieved the experimental work and measurements. All authors checked and confirmed the final revised manuscript.

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تأثير درجة الحرارة في النمو والتكاثر والعمر والفقد في وزن الحبوب لخنفساء الخابـــــرا *Trogoderma granarium*

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الملخص :

خنفساء الخابرا *Trogoderma granarium* (Coleoptera: Dermestidae) هي من الأنواع العالمية ومن أكثر الآفات الحشرية تدميراً لمنتجات الحبوب المخزنة، وعشرات السلع الأخرى، ولها أهمية كبيرة، تعد درجة الحرارة محركا رئيسيًا لوظائف الحشرات الرئيسية بما في ذلك التطور والبقاء وطول العمر والتكاثر لذلك تم تصميم هذا العمل لدراسة تأثير أنظمة درجات الحرارة المختلفة (22 °م، 27 °م ، 32 °م ، 37 °م ، و 42 °م) على النمو والتكاثر وطول العمر وفقدان وزن الحبوب لـ *T. granarium* باستخدام حبوب القمح الكاملة كركيزة تغذية، تم استخدام وقت ومعدل النمو لتقدير عتبة النمو الأدنى (T0) ثم أيام الدرجة (dd's) المطلوبة للمنافسة على التطوير. كان لدرجة الحرارة تأثيرات كبيرة على النمو الكلي، وطول العمر، ومدة الحياة، والخصوبة، وفقدان الوزن لـ *T. granarium* باستثناء درجة حرارة 42 °م ، زادت معدلات البقاء على قيد الحياة في المراحل غير الناضجة مع زيادة درجة الحرارة. كذلك كانت النسبة بين الجنسين متحيزة بالنسبة للإناث مع ارتفاع درجة الحرارة من 22 °م إلى 37 °م ، ولكن عند 42 °م كانت النسبة بين الجنسين متحيزة بالنسبة للذكور. تم تسجيل أدنى (T0) لعمر الذكور، يليه لعمر الأنثى. في المتوسط تحتاج دورة الحياة الإجمالية وفترات حياة الإناث والذكور لخنافس *T.granarium* إلى 602.0 ± 15.08، و938.14 ± 31.86، و950.23 ± 22.34 يوم على التوالي لإكمال تطورها. توصي هذه الدراسة تجار الجملة باستخدام درجة حرارة 42 °م أو أعلى لحماية القمح المخزن، لأنها تزيد من معدلات النفوق، وتقلل الخصوبة وطول العمر، وتقلل من فقدان وزن القمح بواسطة *T. granarium*.

الكلمات المفتاحية:

أيام الدرجة، طول العمر، عتبة النمو المنخفضة، البقاء، القمح

Table 1: Mean (± SE) of development, longevity, weight loss, and reproduction of the Khapra beetle, *Trogoderma granarium* at various temperature regimes

Biological aspects		Temperature (°C)				
		22	27	32	37	42
Development (Egg-Pupa)		40.1 ± 0.64 a	33.90 ±0.61 b	30.70 ± 0.47 c	19.70 ± 0.73 d	12.90 ±0.61 e
Total Development (Egg-Adult)		47.0 ± 0.89 a	41.10 ± 0.66 b	38.50 ± 0.56 c	27.80 ± 0.92 d	17.70 ± 0.82 e
Immature survival rate		0.71	0.72	0.78	0.81	0.48
Sex ratio (♂ : ♀)		1: 1.15	1:1.12	1:1.11	1: 1.08	1: 0.84
Female longevity (d)	Preoviposition period	4.40 ± 0.25 a	4.0 ± 0.32 a	3.0 ± 0.32 b	2.40 ± 0.25 b	2.0 ± 0.32 bc
	Oviposition period	12.20 ± 0.37 a	10.80 ± 0.74 ab	9.40 ± 0.51 b	10.40 ± 0.81 ab	6.60 ± 0.68 b
	Postoviposition period	3.80 ± 0.37 a	3.40 ± 0.25 b	2.60 ± 0.51 b	1.60 ± 0.40 bc	0.60 ± 0.25 c
	Total longevity	20.40 ± 0.81 a	18.20 ± 0.58 a	15.0 ± 0.74 b	13.60 ± 1.40 b	9.20 ± 0.86 b
Male longevity (d)		17.60 ± 1.07 a	16.40 ± 0.51 a	13.80 ± 0.66 b	10.40 ± 0.81 bc	8.60 ± 1.03 c
Life span (d)	Female	67.40 ± 1.96 a	59.30 ± 1.24 b	53.5 ± 1.30 c	41.40 ± 2.32 d	26.90 ± 1.68 e
	Male	64.60 ± 1.96 a	57.50 ± 1.70 b	52.3 ± 1.22 c	38.20 ± 1.73 d	26.30 ± 1.85 e
Weight loss (g)		0.77 ± 0.04 b	0.85 ± 0.04 b	1.17 ± 0.07 a	1.27 ± 0.05 a	0.59 ± 0.04 c
Weight loss%		15.4	17.0	23.4	25.4	11.8
Healthy grain (g)		4.33 ± 0.04 b	4.15 ± 0.04 b	3.83 ± 0.07 a	3.73 ± 0.05 a	4.41 ± 0.04 c
Healthy grain%		84.6	83.0	76.6	74.6	88.2
Fecundity/female		23.20 ± 2.59 cd	26.60 ± 2.62 c	42.0 ± 1.76 b	50.8 ± 2.15 a	19.0 ± 2.84 d

Table 2: Lower developmental threshold (T_0) and coefficient of determination (R^2) for development of immature stages (egg-pupa) and total development (Egg-adult) for the Khapra beetle, *Trogoderma granarium*

Development		Equation	R^2	T_0
Total development of immature stages		y = - 0.0416 + 0.0026 ×	0.85	16.00
Total Development (Egg-Adult)		y = - 0.0211 + 0.0017 ×	0.82	12.41
Life span	Female	y = - 0.0109 + 0.0010 ×	0.84	10.90
	Male	y = - 0.0112 + 0.0011 ×	0.86	10.18

Table 3: Thermal requirements (± SE) for development (DDs) of the Khapra beetles, *Trogoderma granarium*, at various temperature regimes

Development		Temperature (°C)					Mean ± SE
		22	27	32	37	42	
Total development (Egg-Pupa)		240.60 ± 03.84 e	372.90 ± 06.65 c	491.20 ± 07.56 a	413.70 ± 15.35 b	335.40 ± 15.72 d	370.76 ± 9.82
Total Development (Egg-Adult)		452.65 ± 08.06 e	599.65 ± 09.59 c	754.22 ± 11.02 a	683.60 ± 22.53 b	523.74 ± 24.18 d	602.77 ± 15.08
Life span	Female	741.48 ± 18.37 c	956.34 ± 25.25 b	1126.74 ± 22.73 a	1038.78 ± 46.25 ab	827.26 ± 46.25 c	938.14 ± 31.86
	Male	775.39 ± 14.28 c	972.19 ± 13.46 b	1143.37 ± 05.34 a	1013.79 ± 40.14 b	846.41 ± 38.45 c	950.23± 22.34